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Historical processes constrain metacommunity structure by shaping different pools of invertebrate taxa within the Orinoco basin

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Abstract

Aim: To identify and characterize the distribution of invertebrate taxa in the Orinoco basin and how their distribution affects the metacommunity structure along the river network.

Location: Meta and Guaviare sub-basins, Orinoco basin, Colombia, South America.

Methods: We characterized the invertebrate communities and environmental characteristics of 25 streams from six ecoregions in the Orinoco basin. The ecoregions present different historical evolution, altitude, slope, climate and vegetation features. We used multiplicative diversity partitioning to compare the contributions of riffle (α and $\beta 1$), stream ($\beta 2$) and ecoregional ($\beta 3$) scales to the overall gamma diversity of the basin. We also applied the Elements of Metacommunity Structure framework to delineate metacommunity types and a distance-based redundancy analysis to assess the relative relevance of environmental, spatial and ecoregional drivers in species compositions of invertebrate communities.

Results: Streams showed significant differences in community composition among the ecoregions. Several discrete pools of invertebrate taxa occurred in the basin that largely matched the distribution of the ecoregions. Consequently, the metacommunity in the basin resembled a Clementsian idealized structure. The species composition of invertebrate communities was mostly explained by ecoregion type and its interaction with the local environment, particularly its physiographic features.

Main conclusions: Historical and evolutionary processes have resulted in species pools differing between the ecoregions of the Orinoco basin. At the basin scale, the metacommunity structure seems to be constrained by ecoregional features rather than by spatial structure or the local environment. Hence, using the basin as a unit for biodiversity conservation and river management would not adequately reflect the diversity and distribution patterns in highly heterogeneous basins such as the Orinoco basin.

KEYWORDS

assembly process, beta diversity, Colombia, diversity partitioning, ecoregion, historical events

1 | INTRODUCTION

Basins have been considered an appropriate scale to unravel the metacommunity assembly process in riverine ecosystems (Brown & Swan, 2010; Cañedo-Argüelles et al., 2015; Grönroos et al., 2013). In a metacommunity context, tributary communities are viewed as subsets of a regional species pool whose species composition is shaped by environmental sorting, dispersal-driven processes and stochastic events. As they partly or completely encompass a river network within a delimited area, a species pool common to all the tributary communities is usually expected (Brown & Swan, 2010). However, a unique species pool cannot always be assumed to occur across the basin (Higgins, Bryer, Khoury, & Fitzhugh, 2005). Historical events, such as those that occurred during the Tertiary and Quaternary periods, could lead to the development of several species pools that are patchily distributed within basins or sub-basins (Hoorn et al., 2010; Hubert & Renno, 2006).

The metacommunity framework allows assessment of the role of historical, regional, spatial and environmental factors in the assembly process across scales (Leibold & Chase, 2018; Mittelbach & Schemske, 2015). In recent decades, the use of pattern-based statistical methods, such as the analysis of the Elements of Metacommunity Structure ("EMS," Leibold & Mikkelson, 2002) and direct ordination approaches (e.g., distance-based redundancy analysis [dbRDA], Legendre & Anderson, 1999), has helped to disentangle the main drivers of metacommunity structure and dynamics (Leibold & Chase, 2018). The major constraints for metacommunities at the basin scale, for instance, include environmental sorting, the dendritic structure of the river network and its effects on habitat connectivity, and the dispersal ability of the species (e.g., Brown & Swan, 2010; Cañedo-Argüelles et al., 2015; Grönroos et al., 2013; Sarremejane, Mykrä, Bonada, Aroviita, & Muotka, 2017). However, the influence of these processes on metacommunity structure may be affected by the occurrence of distinct pools of species in the basin (Benito, Fritz, Steinitz-Kannan, Vélez, & Mcglue, 2018).

A "pool" or "regional pool" of species refers to the set of all species available to colonize local communities (Srivastava, 1999). Since the introduction of this concept in the Theory of Island Biogeography, species pools have helped to disentangle the relative contributions of local, regional and historical factors to shaping metacommunity structure (Cornell & Harrison, 2014). An accurate characterization of species pools can help to determine how large-scale forces interact with local constraints to shape the species composition of local communities and metacommunities across different scales (Cornell & Harrison, 2014; Ricklefs, 1987). Indeed, almost all analyses to address the assembly process (e.g., null models or EMS) depend on how the species pool is defined in its composition and spatial extent (Buschke, Brendonck, & Vanschoenwinkel, 2014; Lessard et al., 2012). Hence, the appropriate characterization of the species pool(s) should be the first step towards understanding the assembly process (Cornell & Harrison, 2014).

In the Neotropical region, geological and climatic events such as Andean uplifts and glacier retreats have shaped unique combinations of river forms and riparian ecosystems at the ecoregional scale (Hoorn et al., 2010; Rull, 2008). For example, when descending from the Andes to the Amazon, there is a matrix of streams with constrained channels that are surrounded by shrubs in the Páramo, followed by rivers with gorge channels and steep slopes in the Andean-cloud forest and Piedmont regions, and then meandering rivers surrounded by well-developed rainforest in the Amazonian region. As these ecoregional features do not always match the extension of the stream networks, this scenario provides the opportunity to test the influence of the potential occurrence of different pools of species metacommunity structure. The few comparable studies carried out in the Tropics have indicated the occurrence of several pools of species across the region (Benito et al., 2018; Brasil, Vieira, Oliveira-Junior, Dias-Silva, & Juen, 2017; Datry et al., 2017). However, to our knowledge only one has addressed how the occurrence of different pools of species may shape the structure of phytoplankton metacommunities (Benito et al., 2018). This study, however, included a community of poor dispersers in disconnected systems (Andean lakes), which lead to clumped dispersion patterns in species distribution (Vilmi, Karjalainen, & Heino, 2017).

In this study, we characterized the distribution of invertebrate species pools in the Orinoco basin and how their distribution affects the structure of the metacommunity across the stream network of the basin. In the absence of major disturbances, these patterns may provide an appropriate comparator to shed light on the effects of deforestation, mining, damming and intensive agriculture on the biodiversity in the region (Sabater, González-Trujillo, Elosegi, & Donato Rondón, 2017). We hypothesized that if evolutionary history influenced the structure of freshwater communities in parallel with ecoregions' physiography and geomorphological structure, a nearly discrete species pool would characterize each ecoregion. If this was the case, beta diversity would be greater between ecoregions than between streams of the same ecoregion. To test this hypothesis, we characterized and compared invertebrate communities from six different ecoregions in the Orinoco basin. These ecoregions differ in their historical evolution, current climates, vegetation cover, and riverine channel form and slope (Table 1).

2 | METHODS

2.1 | Study area

The Orinoco basin is the third largest basin in South America, covering an area of about 990,000 km^2 that is in most of Venezuela and in the eastern part of Colombia (Romero Ruíz, Galindo García, Otero García, & Armenteras Pascual, 2004). The complex geological and climatic history of the basin has shaped a broad range of ecosystems across heterogeneous landscapes (Romero Ruíz et al., 2004). The geological and climatic events of the Late Miocene and Pliocene, in particular, have shaped the current physiographic features and ecoregions (e.g., Goosen, 1971; van der Hammen, 1974; Hoorn et al., 2010; Hughes & Eastwood, 2006). Within the basin, there is an intricate network of rivers and tributaries, spanning from

TABLE 1 Physiographic features of the six ecoregions in the Orinoco basin that were assessed in the present study

	Páramo	High-Andean	Piedmont	Alluvial fans	High Plains	Guiana shield	References
Age of major landform	Early Pleistocene to Holocene	Early Pleistocene to Holocene	Pliocene to early Holocene	Pliocene to Holocene	Early Holocene	Miocene	Flórez (2003), Goosen (1971), van der Hammen (1974, 1974), Restrepo and Toussaint (1988)
Altitude (m asl)	>3,000	2,000–3,000	300–1,000	<300	<400	<500	van der Hammen (1974, *personal observations*)
Vegetation type	Páramo and subPáramo	Andean forest	Lower tropical forest	Lower tropical forest	Savanna and Gallery forest	Dry tropical woodland	van der Hammen (1974)
Climate	Tundra (ET)	Oceanic (Cfb)	Rainforest (Af)	Rainforest (Af)	Monsoon (Am)	Monsoon (Am)	Köppen-Geiger classification (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006)
Channel form	Gorge	Mountain	Mountain	Braided	Meandering	Meandering	sensu Petts & Amoros, 1996
Slope	Medium	Medium-high	High	Low-medium	Low	Low	
Streambed main substratum	Cobble	Boulder and cobble	Boulder and cobble	Cobble and gravel	Sand	Bedrock	

Note: The features included are recognizable at a large spatial scale.

0 to 3,500 m a.s.l, and three constraining relief forms: ancient massifs and shields, recently raised ridges, and tectonic depressions or accumulation plains (Stallard, 1985). The water chemistry of the streams and rivers is primarily determined by the geological features (Stallard, 1985), while historical events have contributed to shaping riverscape biodiversity (Říčan, 2011).

We sampled aquatic invertebrates at 25 stream segments within an area of about 40,000 km^2 in the Colombian Orinoco (Figure 1). The area encompassed a broad altitudinal gradient (from 300 to 3,400 m a.s.l) to include a largely heterogeneous area. Our sampling sites were distributed among six ecoregions of the Orinoco basin, with 3–7 streams selected in each ecoregion according to their geomorphological/physiographical comparability (see Table 1) and with no signs of anthropogenic impact. We selected only pristine or near-pristine streams. A larger number of streams were sampled in the ecoregions with greater variability (i.e., alluvial fans n = 4, high-Andean n = 5, Piedmont n = 7), based on pre-survey data.

2.2 | Environmental characterization of the streams

Environmental descriptors for each stream segment included hydrology, substratum and water quality (Table 2). Longer-term hydrological variables were estimated using the rational method modified by Témez (2003). This method estimates a stream's water flow as function of the total precipitation, the basin area and associated land uses, the time of concentration and the runoff coefficient (Supplementary Material). Once the daily water flow had been determined, we estimated the threshold at which the stream's basal flow was surpassed, as a unit of disturbance for the invertebrate communities. We then calculated: (a) the number of days elapsed since the last flood event (defined as the one doubling the basal flow discharge); (b) the number of flood events; and (c) the ratio between the maximum and basal flow discharges.

In each stream segment (100–200 m long), we selected three riffle areas that were representative of the range of substratum types, flow velocities, channel widths and depths, and canopy cover occurring along the stream. Physical and chemical variables were measured during invertebrate sampling (January–February 2017) and on two further occasions (November 2016 and, January–February 2018), that corresponded to high and low water flows, respectively. Instantaneous discharge was estimated in the three riffles by measuring of water depth and flow velocity at 15 cm intervals along three cross sections. At each interval, we also recorded the dominant substrate. Flow velocity was measured with a digital flow meter (SCHILTKNECHT—MiniAir 20). Canopy shading (%) was estimated from vertical photographs using a fisheye lens and subsequent image analysis. Conductivity, pH, oxygen and temperature were recorded using a HANNA HI98194 water quality meter upon arrival (early morning) and departure (dawn) from the site.

On each occasion, 1 L of water was collected for physico-chemical analyses, filtered through 0.7 μm glass fibre filters (Whatman GF/F) and stored frozen until analysis. In the laboratory, ammonium and nitrate concentrations were determined on a Dionex ICS-5000 ion chromatography system (Dionex Corporation). Reactive phosphorus (PRS) concentrations were determined colorimetrically using the fully automated discrete analyzer Smartchem 140 (AMS Allaince). Total suspended solids (TSS) were analysed by filtering 500 ml of water through a pre-weighed GFF and drying the filtrate for 1 hr at 105°C. The mean and coefficient of variation of all the variables per ecoregion are summarized in Table S1.

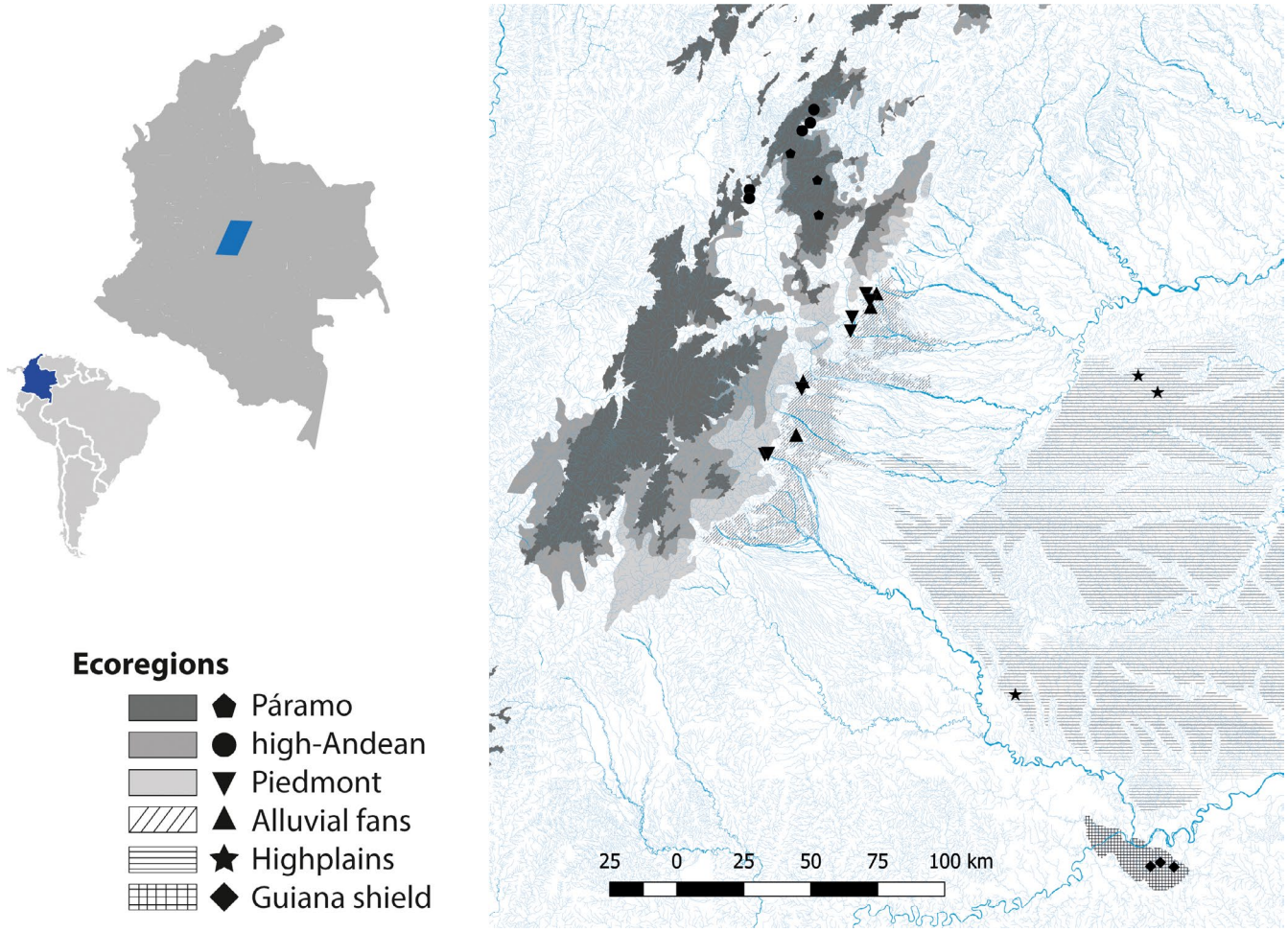

FIGURE 1 Geographical area of the ecoregions and the positions of the sampled streams in the Orinoco basin

2.3 | Invertebrate sampling

Stream invertebrates were sampled during the dry season (January–February 2017). Invertebrates were collected using a multi-habitat sampling procedure, with five Surber (mesh size: 350 µm; area: 0.09 m^2) samples collected in stream substrata that were selected according to their corresponding habitat coverage. For instance, if a riffle was composed of 60% of boulders, 30% gravel and 10% cobbles, three Surber samples of the first, one of the second and one of the third substratum type were collected. The substratum distribution in each riffle was evaluated visually using the Wentworth scale (mm, diameter-based) as a reference (Wentworth, 1922). We only sampled boulders (diameter >250 mm) smaller than the sample frame. In six of the 25 streams sampled, only two riffle sections (10 Surber samples) were sampled because of problems with access. Our final dataset comprised a total of 343 Surber samples (six ecoregions, 25 streams and 69 riffle sections).

In the laboratory, invertebrates were sorted and identified to the genus level, following Trivinho-Strixino and Strixino (1995), Merritt and Cummins (2008), Domínguez and Fernández (2009) and González-Córdoba, Carmen Zúñiga, and Manzo (2015). Chironomidae and Ephemeroptera were dissected and mounted in Euparal® following the protocol of Domínguez (2006) and Andersen, Cranston, and Epler (2013), respectively. The pupae of Chironomidae were mounted to confirm some taxonomical identities (Prat, González-Trujillo, & Ospina-Torres, 2014).

2.4 | Data analyses

We used a four-step approach to (a) explore the relative contribution of different spatial scales to the overall basin (gamma) diversity; (b) test for significant differences in environmental and community composition variability among and within ecoregions; (c) assess the EMS (Leibold & Mikkelson, 2002) by matching the observed patterns to an idealized model; and (d) quantify the relative contribution of environmental conditions, spatial structure and ecoregional identity to explaining metacommunity structure.

2.4.1 | Additive partitioning of diversity

The additive partitioning of diversity (Whittaker, 1972) has been used to test the uniformity of diversity across spatial scales or across patches within a matrix (Lande, 1996). This approach accounts for the compositional differentiation of groups (e.g., patches) by partitioning

TABLE 2 Water quality and physiographic variables used for modelling the environmental component in dbRDA models

Dataset	Scale	Variable
Water quality	Riffle-level	Conductivity
		pH
		Saturated Oxygen
		Reactive phosphorus soluble—PRS
		Total organic carbon—TOC
		Canopy shading
		Total suspended solids—TSS
		Ammonium—N-NH_4
		Nitrate—N-NO_3
Physiography	Stream-level	Elevation
		Slope
		Temperature—T
		Cross-sectional channel width—W
		Average depth
		Average flow velocity
		Instantaneous discharge—Q
		Max. discharge/ Inst. Discharge—Qmax.Q
		Number of days after the last spate—nEvents2tQ
		Number of spate events—n2tQdays
		Percentage of low mobile substrate (>Boulders)
		Percentage of mid mobile substrate (Pebble-Boulders)
		Percentage of high mobile substrate (<Pebble)

the regional or gamma (γ) diversity into within- and between-group components, representing the alpha (α) and beta (β) diversities, respectively (Jost, 2007). Thus, if diversity is uniformly distributed, the ratio between the alpha and gamma components will have a value of 1 (Lande, 1996). We used the approach of Crist, Veech, Gering, and Summerville (2003) to include distinct spatial scales in a hierarchical sampling design, the lower sampling levels being nested within higher levels. By doing this, the gamma (γ) diversity can be expressed as the proportional contributions of diversity due to each level of the hierarchy (Crist et al., 2003). In our hierarchical sampling design, the highest level corresponded to the Orinoco basin, with its gamma diversity partitioned within (α) and among riffles of each stream (β1), among streams of each ecoregion (β2) and among ecoregions within the basin (β3). The sum of α + β1 + β2 + β3 is equivalent to γ.

Additive partitioning can be conducted on the most widely used diversity metrics: species richness, the Shannon entropy index and the Gini–Simpson index (Jost, 2007; Lande, 1996). We used only the species richness and the Shannon entropy because these are the two metrics that increase in line with the compositional differentiation in the additive partitioning framework (Jost et al., 2010). Under this framework, compositional differentiation estimates how much diversity is added (by the occurrence of different species and the increasing in their respective abundances) at each hierarchical level. For instance, the additive species richness β3 is a measure of the average number of species from the Orinoco basin (γ) absent from a "sample" taken at the ecoregional level. The expected diversity at each level was calculated 9,999 times by individual-based randomization of the community matrix (see Crist et al., 2003 for further details on the formulas and calculations). We performed all the calculations using the "adipart" function of the VEGAN package (Oksanen et al., 2013).

2.4.2 | Environmental and community composition variability at the ecoregional scale

Following Heino et al. (2013), we used both the canonical analysis of principal coordinates (CAP, Anderson & Willis, 2003) and the test for homogeneity of dispersion (PERMDISP, Anderson, 2006) to assess variability in community composition and environmental conditions among and within ecoregions. Community data were pooled at the riffle level (summing up the counts of five Surber samples) in order to match the scale at which environmental variables were measured at each stream. CAP identifies the axes through the multivariate space that best discriminate among a priori groups. In our case, we allocated riffles to correct ecoregion types (leave-one-out procedure) and test for among-ecoregion differences in community composition using random permutations. A total of 9,999 permutations were run to test the null hypothesis that ecoregion centroids do not differ. We used the Euclidean distance for standardized environmental variables and the Hellinger distance (Legendre & Gallagher, 2001) with the invertebrate incidence- and abundance-based data. We calculated the Hellinger distance for the incidence- and abundance-based data to maintain comparability with the redundancy analysis. Before analysis, we ran diagnostic tests to guarantee the best discrimination among the ecoregions. We used PERMDISP to estimate the within-ecoregion dissimilarity and to compare among-ecoregion differences in the distance between the observations and the group centroid. The significance of the among-group differences was tested with permutation tests for least-squares residuals. The null hypothesis of no differences the among ecoregions in terms of environmental and community dissimilarity was tested using a permutation test with 9,999 runs. We performed CAP calculations with the "CAPdiscrim" function of the BiodiversityR package (Kindt & Kindt, 2018) and PERMIDISP tests with the "betadisper" function of the VEGAN package (Oksanen et al., 2013).

2.4.3 | Elements of metacommunity structure

The analysis of the EMS determines which idealized metacommunity structure (Leibold & Mikkelson, 2002) or quasi-structure (Presley, Higgins, & Willig, 2010) best fits the observations obtained from the community matrix. Based on a species-by-site incidence matrix, in which sites are rearranged by similarities in species composition and species are rearranged by similarities in distribution (Leibold & Mikkelson, 2002), EMS analysis assesses the coherence, turnover and boundary clumping of species

distributions, looking for the best-fit model. By ordering the matrix, the sites with similar species composition are located closer to one another, and, in a similar way, the species with similar occurrence among the sites are closer to one another (Gauch, 1982). Coherence is assessed by counting the number of embedded absences in the ordinated matrix and by comparing that value to a null distribution of embedded absences (i.e., a checkerboard distribution with gaps in the species range). If the number of absences is significantly less than that occurring at random, then the turnover is evaluated. Turnover is assessed by counting the number of species replacements along the matrix and comparing that value to the null distribution. A significant negative turnover suggests a nested distribution, whereas a significant positive turnover suggests an evenly spaced, Clementsian or Gleasonian structure. Finally, boundary clumping was evaluated using Morisita's dispersion index and subsequently tested against expected distributions using a chi-squared test. Values significantly greater than one indicate clumped range boundaries, and values significantly less than one indicate hyperdispersed range boundaries, while equalling one indicate randomly distributed range boundaries.

We used the "Metacommunity" function of the METACOM package (Dallas, 2014) to perform all EMS analyses. EMS can be sensitive to the grain size (Marcilio-Silva, Zwiener, & Marques, 2017); therefore, we created two datasets with different grain sizes (corresponding to the riffle and stream levels). The selected null model constrained the species of richness of each riffle or stream to equal empirical richness, with equiprobable occurrences for each species. It corresponded to the "r1" option in the function. This null model has a more desirable combination of type I and type II error properties than Random 0 or Random 4 (Gotelli, 2000; Gotelli & Graves, 1996)

TABLE 3 Additive partitioning of invertebrate diversity in the Orinoco basin, Colombia

	ORINOCO BASIN (n = 25)			
	Observed	Expected	(%)	p-value
Taxa richness—S				
α—within riffles	30.33	100.34	22.8	<.001
β—among riffles	8.22	15.08	6.2	<.001
β—among streams	25.44	12.99	19.1	<.001
β—among ecoregions	69	4.61	51.9	<.001
γ	133			
Shannon Index—H'				
α—within riffles	2.26	3.33	67.1	<.001
β—among riffles	0.07	0.02	2.1	<.001
β—among streams	0.49	0.01	14.5	<.001
β—among ecoregions	0.55	0.004	16.3	<.001
γ	3.37			

Note: The expected values for both taxon richness and Shannon's index correspond to the average values of the null distribution.

and has been successfully used in analysing coherence (e.g., Presley & Willig, 2010). All null models were based on 9,999 permutations.

2.4.4 | dBRDA and variance partitioning

The relative contribution of the environmental variables, spatial structure and ecoregional identity on metacommunity composition was quantified with the dbRDA (Legendre & Anderson, 1999), followed by variation partitioning analysis (Borcard, Legendre, & Drapeau, 1992). Before analysis, community data were pooled at the riffle level (summing up the counts of five Surber samples) in order to match the scale at which environmental variables were measured at each stream. Community data were Hellinger-transformed, and environmental variables were standardized to have a mean 0 and variance 1, as recommended by Legendre and Gallagher (2001) and Legendre and Legendre (2012). The significance of all the models was tested using 9,999 permutations. dbRDA and variance partitioning analysis were performed using the "rda" and "varpart" functions of the VEGAN package (Oksanen et al., 2013), respectively.

We aimed to identify the influence of local environmental variables by using two datasets, one of which included nine water quality variables (including canopy cover) while the other included 13 physiographic variables (Table 2). The most significant variables were retained through a forward selection procedure using the "ordiR2step" function of the VEGAN package (Oksanen et al., 2013). Moran's eigenvector maps (MEMs) were used to model the spatial structure of the streams within each ecoregion (Legendre & Legendre, 2012). Following the method of Declerck, Coronel, Legendre, and Brendonck (2011), the resulting eigenvector maps were arranged in blocks in a staggered matrix, each block corresponding to a distinct ecoregion. MEMs model the spatial dependence in a set of locations as an orthogonal combination of MEM variables derived from geographical coordinates, the number of ecoregions ("blocks") and the stream within each ecoregion (Declerck et al., 2011). We used the "create.dbMEM.model" function of the "adespatial" package (Dray et al., 2018) to create the MEM model. Finally, to identify possible biogeographical effects, we created a matrix of six dummy variables representing the respective ecoregions.

All analyses and graphical outputs were performed using the R statistical software version 3.4.1 (R Core Team, 2018).

3 | RESULTS

We identified a total of 69,206 individuals from 133 genera belonging to 52 families and 14 orders. Rarefaction analysis indicated that the ecoregions were well sampled, as the curves approached the asymptote (Figure S1). The most diverse ecoregion in terms of taxon richness was the high-Andean (74 genera among streams and 43 genera on average per stream), followed by the High Plains (73 genera among streams and 33 genera on average per stream), the Piedmont (65 genera among streams and 24 genera on average per stream), the alluvial fans (63 genera among streams and

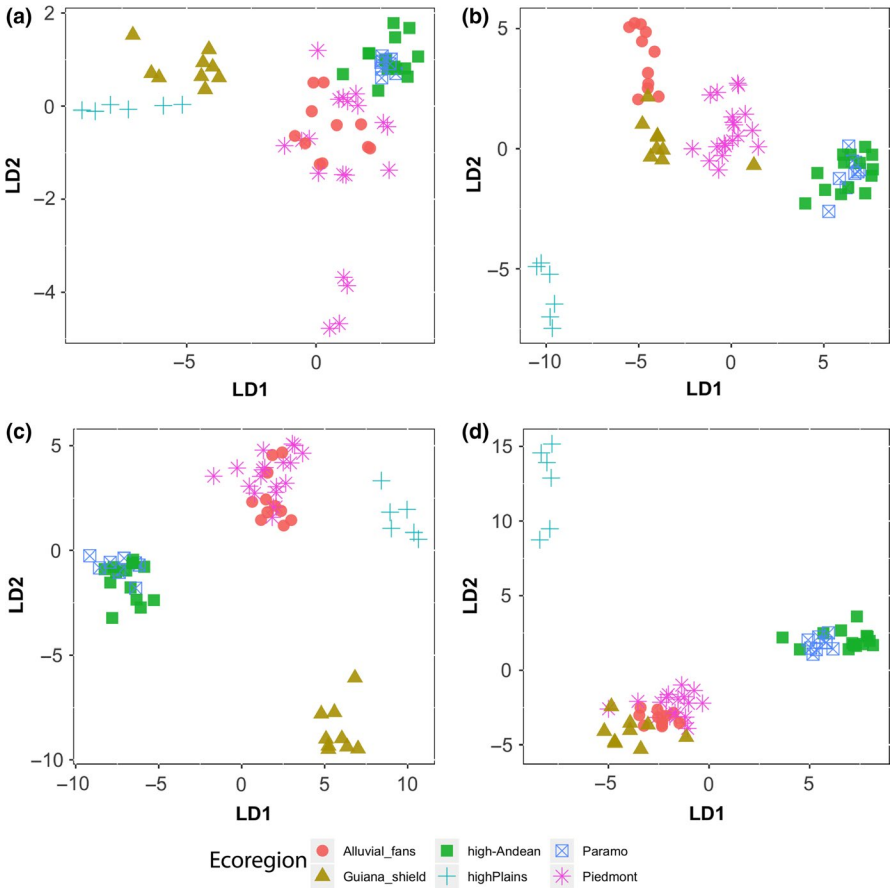

FIGURE 2 Ordination plots of the canonical analysis of principal coordinates (CAP) for (a) water quality data, (b) physiographic variables data, (c) invertebrate incidence-based data and (d) abundance-based data

25 genera on average per stream), the Guiana shield (62 genera among streams and 33 genera on average per stream) and, finally, the Páramo (47 genera among streams and 27 genera on average per stream).

IndVal analysis revealed 67 genera as potential indicators of the ecoregions: eight for the Páramo streams, eight for the high-Andean streams, five for the Piedmont streams, six for the alluvial fan streams, 23 for the High Plains streams and 17 for the Guiana shield streams. Additionally, 28 and seven genera were potential indicators of combinations of two or three ecoregions, respectively (Table S2).

3.1 | Diversity partitioning

Additive partition of diversity based on taxon richness and Shannon's entropy index showed that samples at each riffle (α—*within riffles*) presented lower diversity, on average, than that expected with the null hypothesis (p-value <.001; Table 3), indicating that the taxa are not homogeneously distributed across the spatial scales. Instead, the significantly greater contribution of the upper hierarchical levels ($\beta 2$—among streams, $\beta 3$—among ecoregions) indicated that the non-random clusters of taxa could be separated at larger scales. However, the relative contribution of streams and ecoregions diminished as the more abundant species gained greater weight in Shannon's index estimations. For instance, the component due to ecoregions comprised more than half of the total taxon richness, but less than a quarter of Shannon's diversity index. This decreasing trend suggested that compositional differentiation at the upper levels was mainly due to the presence of unique or low-abundant species in streams and ecoregions.

3.2 | Environmental and community composition variability at the ecoregional scale

We found that invertebrate community composition (Figure 2a–b), water quality (Figure 2c) and stream physiography differed significantly among the ecoregions (Figure 2d); however, classification success rates varied appreciably depending on the dataset. Water quality variables had the lowest discriminant power (66.2%, p-value = .001), followed by physiography (91.2%, p-value = .001), invertebrate abundance (91.2%, p-value = .001) and invertebrate incidence (95.6%, p-value = .001). In all the datasets, the Piedmont and alluvial fan ecoregions had the lowest percentages of correct classification (Table 4). When the invertebrate data were considered, these were the only ecoregions with a percentage of correct classification below 100%.

The PERMDISP tests indicated high variability in community composition and environmental conditions within the ecoregions (Table 4). Environmental and community dissimilarities differed significantly among the ecoregions. In terms of water quality, streams in the Piedmont and alluvial fan ecoregions were the most variable. Streams from the alluvial fans were the most variable in terms of physiography, while streams in the other ecoregions showed similar variability. Regarding community composition, the within-ecoregion

TABLE 4 Percentage of correct classification and mean distance from group centroids for the environmental and community composition data obtained in CAP and PERMDISP analyses, respectively

	Water quality		Physiography		Invertebrate incidence data		Invertebrate abundance data	
Ecoregion	% of correct classification	Mean distance from centroid	% of correct classification	Mean distance from centroid	% of correct classification	Mean distance from centroid	% of correct classification	Mean distance from centroid
Páramo	56	0.6994	67	1.846	100	0.5036	100	0.5415
High-Andean	57	1.5641	93	1.281	100	0.4727	100	0.4839
Piedmont	74	2.6298	100	2.144	89	0.6535	89	0.6379
Alluvial fans	64	2.0423	100	3.502	64	0.6145	91	0.5218
High Plains	67	0.8624	100	1.545	100	0.6044	100	0.5678
Guiana shield	78	1.3404	78	2.123	100	0.5116	100	0.4956
	F	2.9186	F	5.7144	F	16.227	F	3.7336
	p-value	0.018	*p*-value	0.0002	*p*-value	0.001	*p*-value	0.006

Note: The *F*- and *p*-values were obtained from tests for differences in multivariate dispersions among the streams (999 permutations).

variability was similar for both types of data (incidence and abundance). In both datasets, streams in the alluvial fans exhibited the highest within-ecoregion variability.

3.3 | Elements of metacommunity structure

The invertebrate metacommunity of the Colombian Orinoco basin exhibited a Clementsian structure (Table 5). Notably, the EMS analysis results were not affected by data taken at the riffle level or weighted at the stream level. Considering the lower contribution of riffles in the additive diversity partitioning, this result suggests that differences in community structure were negligible within streams. Overall, the invertebrate metacommunity was characterized by a positive coherence, positive turnover and smaller values of boundary clumping. The positive coherence suggests that taxa are exposed to similar environmental gradients, while the positive turnover indicates that community composition along the gradient changes more than would be expected for equiprobable distributions. Finally, the boundary clumping pattern indicates that the compositional changes occur by clusters of taxa.

3.4 | dbRDA and variance partitioning

The variance partitioning revealed that the ecoregional identity and environmental variables were significant predictors of community structure (Figure 3), whereas the effects of spatial structure were not significant. The full models, including water quality, physiographic descriptors and ecoregions, accounted for 48% and 59% of the variation in community composition when using incidence- and abundance-based data, respectively. When taxon abundances were considered, the overall performance of the model increased, but did not affect all the environmental descriptors retained by the forward selection procedure. For both types of data, the most parsimonious models for water quality descriptors included pH, oxygen saturation, TSS, conductivity, PRS and canopy cover. The variables included in the parsimonious model for physiography using the incidence-based data were elevation, slope, substrata with high mobility, channel width and depth, the number of events doubling the basal flow and the number of days elapsed since the last flood event. In the case of the abundance-based data, stream depth was not selected by the forward selection procedure, while flow velocity was selected as a significant variable.

In both models, the greatest amount of variance in the community structure was explained by the ecoregion and its joint effects with physiographic features (Figure 1). When abundances were included, the variance due to water quality increased, while that for the other components decreased. This suggested that water quality had a stronger effect on the distributions of taxon abundance, but its influence on taxon occurrence was weak and depended on physiographic and ecoregional features. These two components exhibited a large amount of shared variance (incidence-based data: 25.1%; abundance-based data: 22.9%), which was even higher than the variance explained by the components individually in both models.

TABLE 5 Elements of metacommunity structure (EMS) analysis of the Orinoco basin using data at the riffle and stream levels

	Coherence				Species turnover				Boundary clumping		
	EAbs	*p*	Mean	*SD*	Rep	*p*	Mean	*SD*	Morisita's Index	*p*	Interpretation
Riffle-level	3,552	<.001	5,778	125	971,995	<.001	577,537	41,615	1.86	<.001	*Clementsian*
Stream-level	1,161	<.001	1910	71	141,731	<.001	89,381	7,114	1.48	<.001	*Clementsian*

Note: These metrics indicated a Clementsian metacommunity structure.

4 | DISCUSSION

Our study used small grain-size samples from across a broad biogeographical area to identify the main drivers of metacommunity structure in the Orinoco basin. At the basin scale, metacommunity structure was shaped by the occurrence of different pools of taxa rather than by spatial structure or the local environment. We found evidence that the distribution of the species pools was substantially shaped by the action of dispersal-limiting processes within historical and ecological timeframes. Our results suggest that events from the Tertiary and Quaternary periods constrained dispersal and shaped discrete pools of invertebrate taxa, while some physiographic features of each ecoregion exerted some control on invertebrate dispersal within the ecological timeframe. Consequently, these results have important implications for the study and conservation of invertebrate metacommunities in a region with high biodiversity (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000).

4.1 | Diversity, distribution and metacommunity structure at the basin scale

The diversity partitioning analysis indicated that the ecoregional level is contributing the greatest to the gamma diversity of the Orinoco basin. CAP and PERMDISP analyses suggested that the dissimilarity in taxon composition is greater among than within ecoregions. These findings demonstrate a patchy distribution within the basin, with each ecoregion having a distinct pool of invertebrate taxa. Previous studies in tropical and subtropical basins found distributions similarly constrained by ecoregion, both in diatom (Benito et al., 2018) and invertebrate (Dedieu, Vigouroux, Cerdan, & Céréghino, 2015; Pero, Hankel, Molineri, & Domínguez, 2019) communities. However, finding this pattern was unexpected in our study given that all the tributaries belong to a single river network.

Previous studies in similar settings have shown that the overall connectedness of the network, as well as the position of each tributary and its particular environmental features, is major determinant of metacommunity structure (e.g., Altermatt, 2013; Brown & Swan, 2010; Finn, Bonada, Múrria, & Hughes, 2011; Grönroos et al., 2013). However, in our study, the lower or no explanatory power of the environment and spatial structure in the dbRDA models and subsequent variance partitioning indicates that other factors may act as the underlying drivers. RDA models usually do not explain a considerable amount of the total variance in community composition, and the variance explained by "pure" spatial or environmental components rarely exceeds 15% (to compare with different assemblages, see Heino, Grönroos, Soininen, Virtanen, & Muotka, 2012). Hence, although the variance was small (R^2_{adj} = 0.1–0.12, percentage of model's explained variance between 19% and 21%, Figure 3), the comparatively higher variance explained by the pure ecoregional component points to ecoregional features as major drivers of community composition. Besides, the higher variance shared with the other components indicates the possibility of a joint effect of ecoregional features and stream environmental conditions on community composition (expanded below).

Taken collectively, the above-mentioned findings suggest that past historical events shaped taxon distribution in the way they shaped the distribution and physiographic features of the ecoregional types across the Orinoco basin (e.g., Goosen, 1971; van der Hammen, 1974; Hoorn et al., 2010; Hughes & Eastwood, 2006). Several studies have indicated that a concordance between species pools and ecoregion (or biogeographical region) distributions provides indirect evidence of the effects of historical events on

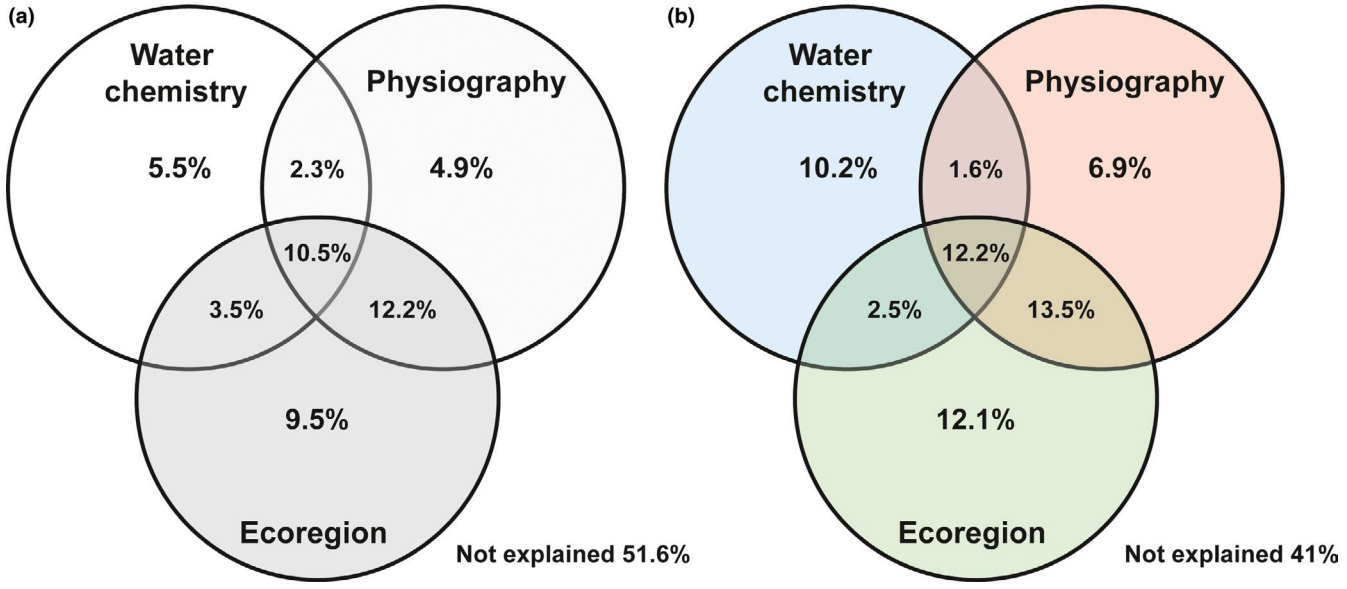

FIGURE 3 Venn diagram showing the variation partitioning results for aquatic invertebrates based on (a) incidence and (b) abundance. The values indicate the proportion of variance (R^2-adjusted) explained by each component and its respective interactions. The spatial component was not significant and was not included in the representation

present-day biodiversity patterns (Brasil et al., 2017; Hazzi, Moreno, Ortiz-Movliav, & Palacio, 2018; Presley & Willig, 2010).

Our EMS analysis results further supported the role of historical events as major drivers. We identified a metacommunity resembling a Clementsian idealized structure (Leibold & Mikkelson, 2002), which suggests that the turnover between the ecoregions is due to changes in clumped sets of associated taxa rather than the responses of individual species. Although the Clementsian idealized structure is rather common in the freshwater realm (Heino, Soininen, Alahuhta, Lappalainen, & Virtanen, 2015), we found no evidence to link the occurrence of this structure with some of the underlying drivers described elsewhere, such as an occurrence of a patchy distribution of resources (Willig et al., 2011), habitat types (Presley, Cisneros, Patterson, & Willig, 2012) and environmental conditions (Tonkin, Sundermann, Jähnig, & Haase, 2015) among the landscapes. Instead, our findings are analogous to those described by Presley and Willig (2010) and Brasil et al. (2017) for Caribbean bat and Amazonian invertebrate communities, respectively. Those studies found that Clementsian idealized structures may stem from the area of origin and the associated specialization of species. Similar clumped patterns in species distributions have been already identified in the tropical Andes and Amazonia (e.g., Hazzi et al., 2018; Hoorn et al., 2010; Hubert & Renno, 2006; Hughes & Eastwood, 2006), with most of these attributable to allopatric speciation by vicariance. For instance, Hughes and Eastwood (2006) found that the clumped distribution of *Lupinus* plants was driven by ecological factors afforded by the emergence of island-like habitats after the Andean uplift. However, further understanding of the historical origin and evolution of the clumped distribution observed in the basin requires defining the phylogenetic relationships between the invertebrate taxa.

The higher turnover among the ecoregions may be attributed not only to historical and evolutionary processes, but also to processes limiting dispersal within an ecological timeframe. Contemporary features of ecoregions, such as climate, landscape topology and stream forms, are a result of past historical events (Goosen, 1971; van der Hammen, 1974). All these features can be viewed as physical boundaries to species dispersal in the present day, helping to explain the considerable amount of variance explained by stream physiography and ecoregional identity in RDA models. Stream discharge, temperature and substrata are examples of the variables conditioned by ecoregion that can influence species dispersal. In the Andean streams, for instance, temperature and the frequency of spate episodes may shape larger scale trends of invertebrate diversity and distribution by limiting species dispersal either physically or physiologically (Gill et al., 2016). Future studies could investigate how species (or genus-level) dispersal ability modulates the effect of the different ecoregional constraints on species occurrence and distribution among river networks. This knowledge will be essential for unravelling the role of evolutionary and ecological processes in shaping the structure of metacommunities in the present day.

The variance partitioning and CAP analyses revealed that the effect of water quality on metacommunity structure is not influenced by the ecoregional context, even when geological differences between the ecoregions are considered. Nevertheless, water quality could be one of the strongest environmental filters explaining beta diversity across streams of some ecoregions. In Piedmont or the alluvial fans, for instance, we observed large variability in water conductivity, as well as in nitrate and total organic carbon (TOC) concentrations. Conductivity may be a strong environmental filter in streams (Cañedo-Argüelles et al., 2012), determining invertebrate occurrence as well as the higher beta diversity observed in streams of these ecoregions. Future studies, including assessing a larger number of streams per ecoregion, could help to determine the role of water quality in the environmental filtering at the ecoregional scale.

4.2 | Implications for metacommunity ecology in riverine ecosystems

The understanding of metacommunity dynamics in riverine ecosystems has been greatly enhanced by considering rivers as dendritic networks (Tonkin, Heino, Altermatt, 2018). As mentioned above, several studies have demonstrated that the branching organization of river networks can strongly affect metacommunity dynamics by regulating dispersal within the river network (Altermatt, Seymour, & Martinez, 2013; Brown & Swan, 2010). However, as far as we know, few studies have addressed how the occurrence of several pools of species can modulate the control exerted by the riverine network in a basin (e.g., Brasil et al., 2017; Tonkin et al., 2015).

Our study indicated that historical events have an important role in the assembly of metacommunities at the basin scale. Particularly, we observed that the occurrence of different regional pools can override the effects of other factors previously described as determinants of metacommunity structure (e.g., local environment or the spatial structure of tributaries). Similar to previous findings in algal communities (Benito et al., 2018), neotropical species distribution seemed to be significantly restricted to each ecoregion or biogeographical district. Hence, the communities that we studied do not constitute a metacommunity in an ecological timeframe or in the basin extent. Conversely, the Orinoco basin can be viewed as a mosaic of functional metacommunity units, with the structure of each unit varying according to the taxa belonging to each species pool and the environmental context at each ecoregion. Brasil et al. (2017) observed a similar context-dependent effect of historical events on the structure of damselfly communities in near-pristine basins from the Amazonas region. However, further studies are needed to determine whether these results can be extended to all Tropical basins.

4.3 | Implications for conservation

One common aim of ecologists and conservationists is to determine how diversity varies over space–time (Jost et al., 2010). In riverine ecosystems, the basin has been used as an appropriate scale to study the causes and consequences of biological diversity (Brown & Swan, 2010; Cañedo-Argüelles et al., 2015; Grönroos et al., 2013). However, as indicated by our results, using the basin may not be appropriate in highly heterogeneous basins such as the Orinoco basin. Before

establishing a conservation unit in tropical basins, a first step should be determining the extent of the pool of species and their relative influence on metacommunity structure. This agrees with the observation of Poiani, Richter, Anderson, and Richter (2000), who reported that the units for conservation should be delineated according to the context of each basin or sub-basin. Our results indicate that such delineation should consider the type and extent of the different ecoregions in the basin, given that Ecoregions harbour distinct pools of species because of historical contingencies. Therefore, they can be considered as functional metacommunity units for assessing biodiversity patterns and designing effective conservation actions.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy restrictions.

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REFERENCES

Altermatt, F. (2013). Diversity in riverine metacommunities: A network perspective. *Aquatic Ecology*, *47*(3), 365–377. https://doi.org/10.1007/s10452-013-9450-3

Altermatt, F., Seymour, M., & Martinez, N. (2013). River network properties shape α-diversity and community similarity patterns of aquatic insect communities across major drainage basins. *Journal of Biogeography*, *40*(12), 2249–2260. https://doi.org/10.1111/jbi.12178

Andersen, P., Cranston, P. S., & Epler, J. H. (2013). *Chironomidae of the Holarctic region: Keys and diagnoses, part 1: Larvae*. Sweden: Entomological Society of Lund.

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, *62*(1), 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x

Anderson, M. J., & Willis, T. J. (2003). Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. *Ecology*, *84*(2), 511–525. https://doi.org/10.1890/0012-9658(2003)084

Benito, X., Fritz, S. C., Steinitz-Kannan, M., Vélez, M. I., & Mcglue, M. M. (2018). Lake regionalization and diatom metacommunity structuring in tropical South America. *Ecology and Evolution*, *8*, 7865–7878. https://doi.org/10.1002/ece3.4305

Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, *73*(3), 1045–1055. https://doi.org/10.2307/1940179

Brasil, L. S., Vieira, T. B., de Oliveira-Junior, J. M. B., Dias-Silva, K., & Juen, L. (2017). Elements of metacommunity structure in Amazonian Zygoptera among streams under different spatial scales and environmental conditions. *Ecology and Evolution*, *7*(9), 3190–3200. https://doi.org/10.1002/ece3.2849

Brown, B. L., & Swan, C. M. (2010). Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology*, *79*(3), 571–580. https://doi.org/10.1111/j.1365-2656.2010.01668.x

Buschke, F., Brendonck, L., & Vanschoenwinkel, B. (2014). Differences between regional and biogeographic species pools highlight the need for multi-scale theories in macroecology. *Frontiers of Biogeography*, *6*(4), fb_23415. https://doi.org/10.5811/westjem.2011.5.6700

Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I., Schriever, T. A., & Lytle, D. A. (2015). Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography*, *42*(4), 778–790. https://doi.org/10.1111/jbi.12457

Cañedo-Argüelles, M., Grantham, T. E., Perrée, I., Rieradevall, M., Céspedes-Sánchez, R., & Prat, N. (2012). Response of stream invertebrates to short-term salinization: A mesocosm approach. *Environmental Pollution*, *166*, 144–151. https://doi.org/10.1016/j.envpol.2012.03.027

Cornell, H. V., & Harrison, S. P. (2014). What are species pools and when are they important? *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 45–67. https://doi.org/10.1146/annurev-ecolsys-120213-091759

Crist, T. O., Veech, J. A., Gering, J. C., & Summerville, K. S. (2003). Partitioning species diversity across landscapes and regions: A hierarchical analysis of a, b, and g diversity. *The American Naturalist*, *162*(6), 734–743.

Dallas, T. (2014). metacom: An R package for the analysis of metacommunity structure. *Ecography*, *37*(4), 402–405. https://doi.org/10.1111/j.1600-0587.2013.00695.x

Datry, T., Vander Vorste, R., Goïtia, E., Moya, N., Campero, M., Rodriguez, F., … Oberdorff, T. (2017). Context-dependent resistance of freshwater invertebrate communities to drying. *Ecology and Evolution*, *7*(9), 3201–3211. https://doi.org/10.1002/ece3.2870

Declerck, S. A. J., Coronel, J. S., Legendre, P., & Brendonck, L. (2011). Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. *Ecography*, *34*(2), 296–305. https://doi.org/10.1111/j.1600-0587.2010.06462.x

Dedieu, N., Vigouroux, R., Cerdan, P., & Céréghino, R. (2015). Invertebrate communities delineate hydro-ecoregions and

respond to anthropogenic disturbance in East-Amazonian streams. *Hydrobiologia*, *742*(1), 95–105. https://doi.org/10.1007/s10750-014-1969-3

Domínguez, E. (2006). *Ephemeroptera of South America*. San Miguel de Tucumán, Argentina: PENSOFT Publishers. Retrieved from https://books.google.es/books?hl=es&lr=&xml:id=dwaJWIe8OfkC&oi=fnd&pg=PA17&dq=dominguez+ephemeroptera&ots=BrLqKCGLEy&sig=Ne6AUcPmb3pO4prg_H995MbtxRE#v=onepage&q=dominguezephemeroptera&f=false

Domínguez, E., & Fernández, H. R. (2009). *Macroinvertebrados bentónicos sudamericanos: Sistemática y biología*. Tucumán: Fundación Miguel Lillo.

Dray, S., Blanchet, G., Borcard, D., Clappe, S., Jombart, G. G. T., Larocque, G., & Wagner, H. H. (2018). *adespatial: Moran's eigenvector maps and related methods for the spatial multiscale analysis of ecological communities*. R package version 0.1-1.

Finn, D. S., Bonada, N., Múrria, C., & Hughes, J. M. (2011). Small but mighty: Headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society*, *30*(4), 963–980. https://doi.org/10.1899/11-012.1

Flórez, A. (2003). *Colombia: evolución de sus relieves y modelados*. Bogotá DC.: Universidad Nacional De Colombia. http://bdigital.unal.edu.co/47989/2/9587013123.PDF

Gauch, H. G. (1982). *Multivariate analysis in community ecology*. Cambridge, UK: Cambridge University Press.

Gill, B. A., Kondratieff, B. C., Casner, K. L., Encalada, A. C., Flecker, A. S., Gannon, D. G., … Funk, W. C. (2016). Cryptic species diversity reveals biogeographic support for the 'mountain passes are higher in the tropics' hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1832), 20160553. https://doi.org/10.1098/rspb.2016.0553

González-Córdoba, M., del Carmen Zúñiga, M., & Manzo, V. (2015). Riqueza genérica y distribución de Elmidae (Insecta: Coleoptera, Byrrhoidea) en el departamento del Valle del Cauca, Colombia. *Biota Colombiana*, *16*(2), 51–74.

Goosen, D. (1971). *Physiography and soils of the Llanos Orientales, Colombia*. Enschede, The Netherlands: International Institute for Aerial Survey and Earth Sciences.

Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, *81*(9), 2606–2621. https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2

Gotelli, N. J., & Graves, G. R. (1996). *Null models in ecology*. Washington, DC: Smithsonian Institution.

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V. L., Kotanen, J., & Bini, L. M. (2013). Metacommunity structuring in stream networks: Roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution*, *3*(13), 4473–4487. https://doi.org/10.1002/ece3.834

Hazzi, N. A., Moreno, J. S., Ortiz-Movliav, C., & Palacio, R. D. (2018). Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences*, *115*(31), 7985–7990. https://doi.org/10.1073/pnas.1803908115

Heino, J., Grönroos, M., Ilmonen, J., Karhu, T., Niva, M., & Paasivirta, L. (2013). Environmental heterogeneity and β diversity of stream macroinvertebrate communities at intermediate spatial scales. *Freshwater Science*, *32*(1), 142–154. https://doi.org/10.1899/12-083.1

Heino, J., Grönroos, M., Soininen, J., Virtanen, R., & Muotka, T. (2012). Context dependency and metacommunity structuring in boreal headwater streams. *Oikos*, *121*(4), 537–544. https://doi.org/10.1111/j.1600-0706.2011.19715.x

Heino, J., Soininen, J., Alahuhta, J., Lappalainen, J., & Virtanen, R. (2015). A comparative analysis of metacommunity types in the freshwater realm. *Ecology and Evolution*, *5*(7), 1525–1537. https://doi.org/10.1002/ece3.1460

Higgins, J. V., Bryer, M. T., Khoury, M. L., & Fitzhugh, T. W. (2005). A freshwater classification approach for biodiversity conservation planning. *Conservation Biology*, *19*(2), 432–445. https://doi.org/10.1111/j.1523-1739.2005.00504.x

Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., … Antonelli, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, *330*, 927–931. https://doi.org/10.1126/science.1194585

Hubert, N., & Renno, J. F. (2006). Historical biogeography of South American freshwater fishes. *Journal of Biogeography*, *33*(8), 1414–1436. https://doi.org/10.1111/j.1365-2699.2006.01518.x

Hughes, C., & Eastwood, R. (2006). Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences*, *103*(27), 10334–10339. https://doi.org/10.1073/pnas.0601928103

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*(10), 2427–2439. https://doi.org/10.1002/ecm.1283

Jost, L., Devries, P., Walla, T., Greeney, H., Chao, A., & Ricotta, C. (2010). Partitioningdiversityforconservationanalyses.*DiversityandDistributions*, *16*(1), 65–76. https://doi.org/10.1111/j.1472-4642.2009.00626.x

Kindt, R., & Kindt, M. R. (2018). *Package 'BiodiversityR'*. Obtenido de http://vps.fmvz.usp.br/CRAN/web/packages/BiodiversityR/BiodiversityR.pdf

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*(3), 259–263. https://doi.org/10.1127/0941-2948/2006/0130

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, *76*(1), 5. https://doi.org/10.2307/3545743

Legendre, P., & Anderson, M. J. (1999). Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, *69*(1), 1–24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), 271–280. https://doi.org/10.1007/s004420100716

Legendre, P., & Legendre, L. (2012). *Numerical ecology*. Amsterdam, The Netherlands: Elsevier.

Leibold, M. A., & Chase, J. M. (2018). *Metacommunity ecology* (1st ed., Vol. *59*). Princeton: Princeton University Press.

Leibold, M. A., & Mikkelson, G. M. (2002). Coherence, species turnover, and boundary clumping: Elements of meta-community structure. *Oikos*, *97*(2), 237–250. https://doi.org/10.1034/j.1600-0706.2002.970210.x

Lessard, J. P., Borregaard, M. K., Fordyce, J. A., Rahbek, C., Weiser, M. D., Dunn, R. R., & Sanders, N. J. (2012). Strong influence of regional species pools on continent-wide structuring of local communities. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1727), 266–274. https://doi.org/10.1098/rspb.2011.0552

Marcilio-Silva, V., Zwiener, V. P., & Marques, M. C. M. (2017). Metacommunity structure, additive partitioning and environmental drivers of woody plants diversity in the Brazilian Atlantic Forest. *Diversity and Distributions*, *23*(10), 1110–1119. https://doi.org/10.1111/ddi.12616

Merritt, R. W., & Cummins, K. W. (2008). *An introduction to the Aquatic insects of North America*. Dubuque, IA: Kendall/Hunt Pub. Co. Retrieved from https://books.google.com.mt/books?xml:id=005FAQAAIAAJ&source=gbs_book_other_versions

Mittelbach, G. G., & Schemske, D. W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends in Ecology & Evolution*, *30*(5), 241–247. https://doi.org/10.1016/j.tree.2015.02.008

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., … Wagner, H. (2013). *Package 'vegan'. Community Ecology Package*, *Version*, *2(9)*.

Pero, E. J. I., Hankel, G. E., Molineri, C., & Domínguez, E. (2019). Correspondence between stream benthic macroinvertebrate assemblages and ecoregions in northwestern Argentina. *Freshwater Science*, *38*(1), 64–76. https://doi.org/10.1086/701467

Petts, G. E., & Amoros, C. (1996). *Fluvial hydrosystems*. London, UK: Chapman & Hall.

Poiani, K. A., Richter, B. D., Anderson, M. G., & Richter, H. E. (2000). Biodiversity Conservation at Multiple Scales: Functional sites, landscapes, and networks. *BioScience*, *50*(2), 133. https://doi.org/10.1641/0006-3568(2000)050[0133:BCAMSF]2.3.CO;2

Prat, N., González-Trujillo, J. D., & Ospina-Torres, R. (2014). Key to chironomid pupal exuviae (Diptera: Chironomidae) of tropical high Andean streams. *Revista De Biologia Tropical*, *62*(4), 1385–1406.

Presley, S. J., Cisneros, L. M., Patterson, B. D., & Willig, M. R. (2012). Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: A comparison of bats, rodents and birds. *Global Ecology and Biogeography*, *21*(10), 968–976. https://doi.org/10.1111/j.1466-8238.2011.00738.x

Presley, S. J., Higgins, C. L., & Willig, M. R. (2010). A comprehensive framework for the evaluation of metacommunity structure. *Oikos*, *119*(6), 908–917. https://doi.org/10.1111/j.1600-0706.2010.18544.x

Presley, S. J., & Willig, M. R. (2010). Bat metacommunity structure on Caribbean islands and the role of endemics. *Global Ecology and Biogeography*, *19*(2), 185–199. https://doi.org/10.1111/j.1466-8238.2009.00505.x

R Core Team. (2018). *R: A language and environment for statistical computing*. ISBN 3-900051-07-0. Retrieved from http://www.R-project.org

Restrepo, J. J., & Toussaint, J. F. (1988). Terranes and continental accretion in the Colombian Andes. *Episodes*, *11*(3), 189–193. https://doi.org/10.18814/epiiugs/1988/v11i3/006

Říčan, O. (2011). *Historical biogeography of neotropical freshwater fishes*. Oxford, UK: Oxford University Press.

Ricklefs, R. (1987). Community diversity: Relative roles of local and regional processes. *Science*, *235*(4785), 167–171. https://doi.org/10.2307/1698957

Romero Ruíz, M. H., Galindo García, G., Otero García, J., & Armenteras Pascual, D. (2004). *Ecosistemas de la cuenca del Orinoco colombiano*. Bogotá, Colomobia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Rull, V. (2008). Speciation timing and neotropical biodiversity: The Tertiary-Quaternary debate in the light of molecular phylogenetic evidence. *Molecular Ecology*, *17*(11), 2722–2729. https://doi.org/10.1111/j.1365-294X.2008.03789.x

Sabater, S., González-Trujillo, J. D., Elosegi, A., & Donato Rondón, J. C. (2017). Colombian ecosystems at the crossroad after the new peace deal. *Biodiversity and Conservation*, *26*(14), 3505–3507. https://doi.org/10.1007/s10531-017-1415-8

Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J., & Muotka, T. (2017). Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshwater Biology*, *62*, 1073–1082. https://doi.org/10.1111/fwb.12926

Srivastava, D. S. (1999). Using local-regional richness plots to test for species saturation- pitfalls and potentials.pdf. *Journal of Animal Ecology*, *68*, 1–16. https://doi.org/10.1046/j.1365-2656.1999.00266.x

Stallard, R. F. (1985). River chemistry, geology, geomorphology, and soils in the Amazon and Orinoco basins. In J. I. Drever (Ed.), *The chemistry of weathering* (pp. 293–316). Dordrecht, The Netherlands: Springer.

Témez, J. R. (2003). Facetas del cálculo hidrometeorológico y estadístico de máximos caudales. *Revista De Obras Públicas*, *3430*, 47–51.

Tonkin, J. D., Heino, J., & Altermatt, F. (2018). Metacommunities in river networks: The importance of network structure and connectivity on patterns and processes. *Freshwater Biology*, *63*, 1–5. https://doi.org/10.1111/fwb.13045

Tonkin, J. D., Sundermann, A., Jähnig, S. C., & Haase, P. (2015). Environmental controls on river assemblages at the regional scale: An application of the elements of metacommunity structure framework. *PLoS ONE*, *10*(8), e0135450. https://doi.org/10.1371/journal.pone.0135450

Trivinho-Strixino, S., & Strixino, G. (1995). *Larvas de Chironomidae (Diptera) do Estado de São Paulo: guia de identificação e diagnose dos gêneros*.

Van der Hammen, T. (1974). The pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography*, *1*(1), 3–26. https://doi.org/10.2307/3038066

van der Hammen, T. (1974). The pleistocene changes of vegetation and climate in tropical South America. *Journal of Biogeography*, *1*(1), 3. https://doi.org/10.2307/3038066

Vilmi, A., Karjalainen, S. M., & Heino, J. (2017). Ecological uniqueness of stream and lake diatom communities shows different macroecological patterns. *Diversity and Distributions*, *23*(9), 1042–1053. https://doi.org/10.1111/ddi.12594

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology*, *30*(5), 377–392. https://doi.org/10.1086/622910

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, *21*(2/3), 213–251. https://doi.org/10.2307/1218190

Willig, M. R., Presley, S. J., Bloch, C. P., Castro-Arellano, I., Cisneros, L. M., Higgins, C. L., & Klingbeil, B. T. (2011). Tropical metacommunities along elevational gradients: Effects of forest type and other environmental factors. *Oikos*, *120*(10), 1497–1508. https://doi.org/10.1111/j.1600-0706.2011.19218.x

BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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